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PETR KOHOUT

Ecology of ericoid mycorrhizal fungi

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Ecology of ericoid mycorrhizal fungi

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Press

Department of Botany, Institute of Ecology and Earth Sciences, Faculty of Science and Technology, University of Tartu, Estonia

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications that are referred in the text by their Roman numerals:

I. Tedersoo L, Abarenkov K, Nilsson RH, Schussler A, Grelet GA, **Kohout P**, Oja J, Bonito GM, Veldre V, Jairus T, Ryberg M, Larsson KH, Kõljalg U. 2011. Tidying Up International Nucleotide Sequence Databases: Ecological, Geographical and Sequence Quality Annotation of ITS Sequences of Mycorrhizal Fungi. *Plos One* 6.

II. Vohník M, Sadowsky JJ, **Kohout P**, Lhotáková Z, Nestby R, Kolařík M. 2012. Novel Root-Fungus Symbiosis in Ericaceae: Sheathed Ericoid Mycorrhiza Formed by a Hitherto Undescribed Basidiomycete with Affinities to Trechisporales. *Plos One* 7.

III. Vohník M, Mrnka L, Lukešová T, Bruzone MC, **Kohout P**, Fehrer J. 2013. The cultivable endophytic community of Norway spruce ectomycorrhizas from microhabitats lacking ericaceous hosts is dominated by ericoid mycorrhizal *Meliniomyces variabilis*. *Fungal Ecology* 6: 281–292.

IV. Lukešová T, **Kohout P**, Větrovský T, Vohník M. 2015. The Potential of Dark Septate Endophytes to Form Root Symbioses with Ectomycorrhizal and Ericoid Mycorrhizal Middle European Forest Plants. *Plos One* 10.

V. **Kohout P**. 2017. Biogeography of Ericoid Mycorrhiza, in: Tedersoo, L. (Ed.), *Biogeography of Mycorrhizal Symbiosis*. Springer International Publishing, pp. 179–193.

VI. **Kohout P**, Tedersoo L. 2017. Effect of soil moisture on root-associated fungal communities of *Erica dominans* in Drakensberg mountains in South Africa. *Mycorrhiza* 27: 397–406.

VII. **Kohout P**, Bahram M, Põlme S, Tedersoo L. 2017. Elevation, space and host plant species structure Ericaceae root-associated fungal communities in Papua New Guinea. *Fungal Ecology* 30: 112–121.

VIII. Põlme S, Bahram M, Jacquemyn H, Kennedy P, **Kohout P**, Moora M, Oja J, Öpik M, Pecoraro L, Tedersoo L. 2018. Host preference and network properties in biotrophic plant–fungal associations. *New Phytologist* 217: 1230–1239.

Author's contribution to each publication:

	I	II	III	IV	V	VI	VII	VIII
Idea and design	–	–	–	**	***	***	*	–
Sampling or data collection	*	–	*	*	***	***	–	*
Molecular analysis	n.a.	*	**	*	n.a.	***	***	n.a.
Data analysis	–	*	*	**	***	***	***	–
Writing	*	**	*	**	***	***	***	*

* moderate contribution, ** high contribution, *** leading role

INTRODUCTION

Mycorrhizal symbiosis is a mutualistic partnership between plants and fungi that represents one of the oldest and the most widespread symbioses on the Earth (Redecker et al. 2000). It has been estimated that approximately 80% of vascular plant species form symbiosis with mycorrhizal fungi (Brundrett 2009). Mycorrhizal fungi play a crucial role in water and nutrient uptake to the host plant. They also enhance host plant defense mechanisms against pathogens and facilitate their growth in environments with high levels of heavy metals. In return, mycorrhizal plants provide carbohydrates, such as glucose and sucrose, to their symbiotic partners (Smith and Read 2008).

Several mycorrhizal types exist that have evolved independently multiple times during evolution for the last 500 million years. Arbuscular mycorrhizas (AM) evolved concurrently with the first colonization of land by plants some 450–500 million years ago, while ectomycorrhizas (EcM) evolved about 200 million years ago (Cairney 2000). One of the youngest mycorrhizal type is ericoid mycorrhizal (ErM) symbiosis, a mutualistic relationship formed between species belonging to several lineages of the Ericaceae family and diverse group of soil fungi. The first appearance of Ericaceae-like plants dates back to 90–75 million years (Nixon and Crepet 1993; Carpenter et al. 2015). It has been hypothesized that ErM symbiosis may have evolved in the same time frame (Cairney 2000). Ericoid mycorrhiza (one of the so-called endomycorrhizal types) is characterized by the intensive fungal colonization of the outermost root cell layer. Mycorrhizal fungi form a coiled intracellular hyphal complex. The fungal hyphae within the plant cell are usually hyaline with a thin cell wall. The plant plasma membrane of the root cells invaginates to envelope the fungal structures, but it is separated from the fungal cell by an interfacial matrix. This represents the interface between the two symbionts, where nutrient exchange takes place (Smith and Read 2008).

Ericoid mycorrhizal plants often occur on extremely poor soils, where most of the nutrients are locked up in complex forms of soil organic matter, with restricted biological availability. The ErM symbiosis represents a key evolutionary adaptation of ErM plants to mobilize the nutrients from such recalcitrant substrates (Kerley and Read 1998). However, ericoid mycorrhiza remains largely overlooked compared to the more common mycorrhizal types, such as AM and EcM, and a broader general understanding of the ErM symbiosis is lacking.

The Ericaceae family comprises 9 subfamilies, 124 genera, and approximately 4,250 species (Kron et al. 2002). Only the basal evolutionary lineages of the Ericaceae, namely, Enkianthoideae, Arbutoideae, Pyroloideae, and Monotropoideae, lack the capability to form ErM. The earliest diverging lineage Enkianthoideae, represented by the sole genus *Enkianthus*, forms arbuscular mycorrhizal symbiosis (Gorman and Starrett 2003; Abe 2005). Instead, species of the Monotropoideae subfamily form the so-called monotropoid mycorrhizal symbiosis (characterized by ectendomycorrhizal anatomical structures) with

specific groups of ectomycorrhizal fungi (EcMF) from the Basidiomycota phylum (Hynson and Bruns 2009), while members of the Arbutoideae and Pyroloideae subfamilies host a wide spectrum of EcM mycobionts in their roots (Krpata et al. 2007). Okuda et al. (2011) described a symbiosis resembling ErM in *Schizocodon soldanelloides* (Diapensiaceae) roots, but this requires independent confirmation. So far, the only sufficiently confirmed ErM plant species belong to the Cassiopoideae, Ericoideae, Harrimanelloideae, Styphelioideae (formally known as Epacridaceae), and Vaccinioideae subfamilies.

Compared to more common mycorrhiza types, such as AM and EcM, our knowledge about the diversity of ericoid mycorrhizal fungi (ErMF) is very superficial. While arbuscular mycorrhizal fungi (AMF) have a monophyletic origin, the ability to form ErM as well as EcM evolved independently multiple times in several fungal lineages (Smith and Read 2008). Earlier attempts to determine fungal diversity were based on direct observations of macroscopic (fungal fruit bodies) as well as microscopic (e.g., spores) structures. These methods allowed researchers to classify AMF to morphospecies based on their chlamydospore anatomy. Similarly, EcMF were classified based on the morphology and anatomy of the EcM colonization structure formed by each individual unique plant-fungal species combination (Agerer 1987–2006). Although these early methods suffered from many drawbacks, their implementation enabled us to classify uncultured fungal species, which would have been completely overlooked and uncommunicated otherwise. Subsequent implementation of molecular methods for fungal species determination boosted up our knowledge of AM as well as EcMF diversity (Öpik et al. 2014; Tedersoo et al. 2010; Tedersoo et al. 2014a). On the other hand, research focused on the ErMF diversity suffered from much more serious drawbacks. Determination of the ErMF lifestyle can neither be based on the phylogenetic affinity to any known lineage as it is the case of AMF and EcMF to some extent nor can ErM lifestyle be defined based on the occurrence of fungal species in Ericaceae root segments, because Ericaceae roots can also harbor non-mycorrhizal fungi (Bougoure and Cairney 2005a, b). Therefore, mycorrhizal resynthesis experiments are needed to describe the character of the association between the host plant and mycobiont and to sufficiently prove the ericoid mycorrhizal lifestyle of Ericaceae-associated mycobionts (Leake and Read 1991). Anatomical features of ErM symbiosis were described above as well as more specifically in Smith and Read (2008). Alternatively, methods applying transmission electron microscopy associated with molecular methods of fungal detection can be used in specific cases (Selosse et al. 2007).

The ErMF belong to several fungal lineages of Ascomycota as well as Basidiomycota. Nowadays, there are few sufficiently proven ErMF, which belong to four taxonomic groups, Helotiales, Chaetothyriales (Ascomycota) and Sebacinales (Basidiomycota) (Allen et al. 2003; Selosse et al. 2007; Tedersoo et al. 2011; Vohník et al. 2016). The most comprehensive knowledge about ericoid mycorrhizal lifestyle in fungi is derived from the *Pezoloma ericae* aggregate (PEA; previously known as *Hymenoscyphus ericae* or *Rhizoscyphus*

ericae aggregate), which contains several species (*Pezoloma ericae* and *Meliniomyces variabilis*) known as ErM symbionts of Ericaceae (Hambleton and Sigler, 2005). Besides the PEA, *Oidiodendron maius* is another well studied ErMF. Its sequenced genome offered the first insights into the evolution of ErM (Kohler et al. 2015).

Our current knowledge about the ErMF diversity and ecology largely relates to the Northern Hemisphere, where PEA (e.g. Vralstad et al. 2002; Usuki et al. 2003; Bougoure et al. 2007; Walker et al. 2011; Gorzelak et al. 2012) or Sebacinales (Allen et al. 2003) often dominate ErMF communities associated with Ericaceae. Compared to the Northern Hemisphere, there are only a few studies addressing ErMF diversity and ecology in the Southern Hemisphere, almost exclusively from Australia (e.g. Williams et al. 2004; Bougoure and Cairney, 2005a,b). These studies showed that Australian Ericaceae interact with distinct species of Helotiales, although some of them are closely related to PEA but distinct such as the recently described *Cairneyella variabilis* (Midgley et al. 2016). On the contrary, *C. variabilis* has never been recorded outside Australia. Much more data is however needed before comprehensive insights into ErMF biogeography can be obtained.

Besides the global distribution of ErMF, composition of Ericaceae root associated fungal communities can be also affected by local environmental factors such as soil chemistry (Hazard et al. 2014), elevation (Gorzelak et al. 2012) and/or vegetation type (Bougoure et al. 2007). Besides that, host identity might also play an important role in structuring mycorrhizal fungal communities (e.g. Vandenkoornhuyse et al., 2002; Sýkorová et al., 2007). Previous studies on host preference in ErM systems provide inconsistent patterns. Although Bougoure et al. (2007) showed differences in ErMF community composition between *Calluna vulgaris* and *Vaccinium myrtillus*, subsequent more inclusive studies recovered no host effect on ErMF communities (Kjoller et al., 2010; Walker et al., 2011). All these studies were conducted at high latitudes, where the diversity of Ericaceae is relatively low. As recently shown, addressing host effect on mycorrhizal fungal communities might have higher significance in regions with higher plant biodiversity, where mycorrhizal fungi might contribute to speciation or species co-occurrence of their host plants (Waterman et al., 2011; Nurfadilah et al., 2013).

Aims and hypothesis

In this thesis, I focus on Ericaceae associated fungi from various aspects of the partnership, because the ericoid mycorrhizal symbiosis is probably the most overlooked mycorrhizal symbiotic type. Firstly, this thesis aims to determine the occurrence of ericoid mycorrhizal life-style among fungi (**I**, **II**, **III**, **IV**). Furthermore, I also focused on determination of environmental factors which significantly affect composition of fungal communities associated with roots of ericoid mycorrhizal plants (**VI**, **VII**, **VIII**). Last but not least, I addressed global distribution and biogeography of ericoid mycorrhizal fungi (**V**).

MATERIALS AND METHODS

Sampling sites and study design

To determine the occurrence of ericoid mycorrhizal life-style among fungi, we chose one sampling site in Norway (**II**) and two sampling sites in Czechia (**III**, **IV**). We repeatedly collected root samples of *Vaccinium myrtillus* in a forest plantation and a nearby natural forest in mid-Norway (**II**). The mats (plants and adhering soil, approx. 40×30×15 cm) of blueberry with some co-occurring *Vaccinium vitis-idaea* were taken from a regenerating *Picea abies* stand. Altogether 20 mats samples were collected between October 2010 and May 2011. Upon receipt in the laboratory, roots were washed free of the adhering substrate and stored at 5 °C until processed. Half of the ericoid roots were used for assessment of fungal colonization (using light microscopy and scanning electron microscopy) and the second half was used for isolation of root associated fungi.

In Czechia, one site was chosen within the Bohemian Forest NP in *P. abies* dominated forest with ericoid understory (*V. myrtillus* and *V. vitis-idaea*). In total, nineteen 3–5 year old spruce seedlings inhabiting different niches within the two sites were sampled on two occasions during the vegetation season (**III**). Seedlings were carefully dug up not to destroy their fine ectomycorrhizal roots, packed in plastic bags and stored at 5 °C until the isolation of the ecto-mycorrhiza-associated fungi on the following day. The second sampling site in Czechia was situated in Bohemian Switzerland NP (**IV**). Fifteen soil samples were collected on the site dominated by *Pinus sylvestris* forest with understory of ericaceous plants (*V. myrtillus*, *V. vitis-idaea* and *Calluna vulgaris*) on podzolic soil. Ericaceae roots were washed under tap water and separated into three fractions: the first part was used for measurement of fungal colonization (using light microscopy), the second part for mycobionts isolation and the third part was used for direct isolation of DNA and subsequent molecular determination of root associated fungi.

To determine the environmental factors, which affect composition of fungal communities associated with roots of ericoid mycorrhizal plants, we sampled roots of Ericaceae plants on Mount Wilhelm in Papua New Guinea (**VI**) and in Drakensberg mountain range in the Republic of South Africa (**VII**). Mount Wilhelm (4509 m.a.s.l.) is located within the Bismarck Range. An elevation transect with six sampling sites (70×70 m) was established in November 2011. The transect was situated on the eastern slope of Mt. Wilhelm at the following elevations: i) 4483 m.a.s.l., ii) 4266 m.a.s.l., iii) 4044 m.a.s.l., iv) 3830 m.a.s.l. v) 3600 m.a.s.l., and vi) 3387 m.a.s.l.. Five separated root samples (each at least 10 m distance from another one) of *Acrothamnus* sp. were taken at each site. For studying the host and spatial effects on putative ericoid mycorrhizal fungi and endophytic fungal diversity, the 3600 m site was chosen, because it had the highest number of Ericaceae species. All collected root samples were cleaned

from the attached soil and dried on silica gel. Each root sample contained 20–25 mg of fresh hair root mass. Roots were transported to a lab where they were refreshed by rinsing in sterile tap water for several minutes. Ericaceae hair roots were surface sterilized in 10% commercial house bleach (3% chlorine) for one minute. The fine roots were subsequently rinsed in sterile tap water, dried and stored at –20 °C. All samples were analyzed separately, without any subsequent pooling.

In Drakensberg mountain range, we selected a study site on a slope of Champagne Castle (**VII**). Dominant vegetation represented open grassland with small patches of primeval forest. We selected nine sites (across an area of 10 km^2). On each site, we established two plots with contrasting soil moisture level. The dry microhabitat with low water content was dominated by sparse vegetation on shallow soils, typically on large erratic boulders with limited access to ground water. We selected a common Ericaceae species (*Erica dominans*), which occurred on all sites in both microhabitats to study differences in root-associated fungal communities. On each, plot one healthy-looking *E. dominans* plant was sampled. All collected root samples were cleaned from the attached soil. Ericaceae hair roots were surface sterilized in 10% commercial house bleach (3% of chlorine) for 1 min and subsequently rinsed in sterile tap water, dried and kept in silica gel. Each root sample contained 20 to 25 mg of fresh fine hair roots.

Data sources

Two studies included in the thesis were based on data collected from publicly available sources, such as the International Nucleotide Sequence Databases consortium (INSDc) (**I**) or publications (**VIII**). Study **I** aimed to extend the trait annotation of fungal INSDc sequences to provide insights into the biodiversity and ecology of mycorrhizal fungi. All fungal sequences (annotated as such in INSDc) of internal transcribed spacer (ITS) of ribosomal DNA (rDNA) were downloaded from INSDc to UNITE (Abarenkov et al. 2010a). Very short sequences (<200 bp) and sequences derived from Next Generation Sequencing techniques – that are normally not allowed in INSD – were excluded. Sequences were annotated by experts on particular mycorrhizal types and/or taxonomic groups. For EcM, AM, ErM and orchid mycorrhizal (OrM) fungi, all representatives of the major mycorrhizal taxonomic groups were retrieved through the use of names of the inclusive taxa as search strings in the organism field in the PlutoF workbench (Abarenkov et al. 2010b). All sequences that were poorly aligned to other species were subjected to bulk megablast searches against INSD and UNITE as implemented in the PlutoF workbench. This enabled us to identify potentially chimeric and reverse complementary sequences as well as sequences belonging to non-targeted taxa. Most of the chimeric and low-quality sequences were discovered by carefully inspecting the alignment. Potentially low-quality sequences were primarily recognized as sequences with unique gaps

and indels in the conserved regions, especially in the 5.8S gene, as compared to their closest sequences. Sequences were also considered of low quality when the beginning or end of the ITS spacers contained >2 obvious substitution errors or indels resulting from inadequate end trimming. Sequences passing the quality control steps were re-aligned with MAFFT; the alignments were corrected manually and subjected to Maximum Likelihood analyses using RAxML (http://phylobench.vital-it.ch/raxml-bb/) or PhyML (ttp://www.bioportal.uio.no/appinfo/show.php?app=phyml) with default options. Sequences with disproportionately long branches were, once again, checked for potential chimeric insertions and low quality.

The second study (**VIII**) aimed to assess the generality of organizational patterns in biotrophic plant–fungal symbioses and builds on individual case studies that were compiled from the Web of Science by combining the search terms 'host specificity', 'host preference' and 'host effect' with 'mycorrhiza' and 'endophytes'. The analysis includes studies in which at least two host plant species were sampled in multiple replicates per study area and fungi were identified using either molecular or morphological methods. In total, we were able to compile 67% datasets out of 73 studies that were regarded as suitable. In most datasets, taxa were delimited using molecular methods and termed as operational taxonomic units (OTUs).

The datasets of plant–fungal associations were categorized into the following guilds: AM, OrM, EcM, ErM, root endophytes and leaf endophytes. For each site, metadata on various geographic, floristic and sampling variables were retrieved from the original publications. Approximate mean annual temperature (MAT) and precipitation (MAP) were retrieved from a high resolution database of the Earth's surface climate (Hijmans et al., 2005) using the software ARCMAP 10.3 (ESRI, Redlands, CA, USA). For each dataset, we calculated the average phylogenetic distance (APD) among hosts using the online phylogenetic query tool Phylomatic (http://phylodiversity.net/phylomatic/).

Isolation of ericoid mycobionts and resynthesis experiments

To determine the occurrence of ericoid mycorrhizal lifestyle in fungi and ecology of ericoid mycorrhizal fungi, we isolated root associated fungi from sampled Ericaceae plants (**II**, **IV**) or seedlings of *P. abies* (**III**). Isolation of Ericaceae was performed from approx. 5-mm pieces of surface-sterilized (30 s in 10% house bleach containing 4.5% of chlorine and rinsed twice in autoclaved water) roots and cultivation on modified Melin Norkrans agar (MMN). All roots were incubated in the dark at 20 °C for 21 days.

Ecological lifestyle of isolated fungi (and other roots associated fungi previously isolated in other studies) was assessed in number of resynthesize experiments with *V. myrtillus* (**II**, **III**, **IV**), *P. abies* (**III**, **IV**) and *Betula pendula*

(**IV**). Seeds of the selected plant species were surface-sterilized with 30% hydrogen peroxide and placed on MMN agar. Non-contaminated seeds were left to germinate for 3 weeks. Lower compartments of split Petri dishes (9 cm in diam.) with perforated central septa were filled with MMN (10x diluted sugars), overlaid with a sterile cellophane membrane to prevent growth of roots into the medium and inoculated with agar plugs cut from margins of colonies of selected fungal isolates actively growing on MMN. The petri dishes with the plugs were left for 3 weeks at room temperature in the dark to produce vegetative mycelium. Then, 3-week-old seedlings were transferred to the dishes, the empty upper compartments accommodating their shoots and the lower compartments their roots. The roots of the seedlings were covered with a piece of sterile moistened filter paper. The dishes were sealed with air-permeable film, lower compartments covered with aluminum foil, and placed in a vertical position in a growth chamber (16/8 hr and 21/15 °C day/night cycle, irradiation 250 μ mol m^{-2} s^{-1}). After 5 months, the plants were extracted and their roots were separated and processed as follows: *V. myrtillus* roots were cleared with 10% KOH (20 min at 121 °C), washed with tap water, acidified (1 min in 3% HCl), washed with tap water, stained with trypan blue (60 min at 121 °C) and de-stained overnight in lactoglycerol; *P. abies* and *B. pendula* roots were hand-sectioned and thin sections were stained with aniline or trypan blue. The stained roots and thin sections were observed using an Olympus BX60 microscope equipped with DIC at high magnification (400x and 1000x).

Molecular analyses

Taxonomic determination of root associated fungal isolates was mostly done by sequencing of ITS region (**II**, **III**). In some cases, small (SSU) or large (LSU) subunits of rDNA were used for more precise phylogenetical placement of the obtained isolates. Fungal DNA was extracted from fresh mycelia using the sorbitol method (Štorchová et al. 2000). DNA amplifications of the rDNA regions were performed using variety of eukaryotic primers. PCR products were checked for length and quality/quantity by gel electrophoresis (1.5% agarose) and purified using the High Pure PCR product purification kit (Roche Holding Ltd, Switzerland). Sanger sequencing was done by GATC Biotech AG (Germany) using the PCR primers, sequence electropherograms were edited manually. The obtained sequences were subjected to BLAST searches and submitted to the GenBank database.

To determine fungal communities associated with Ericaceae roots, we used the 454 pyrosequencing method (**IV**, **VI**, **VII**). Development of high throughput sequencing methods (such as 454 pyrosequencing) enables metagenomic analyses in a manner that exceeds the capacity of traditional Sanger sequencing-based approaches by several orders of magnitude. The DNA of all samples were extracted using a PowerSoil DNA Isolation Kit (MoBio, Carlsbad, CA, USA), following the manufacturer's instructions. For identification of fungi, we

selected the full ITS region (Schoch et al. 2012), amplified with ITS1Fngs, ITS1ngs, and ITS4ngs primers. Each of these primers was supplemented with a 10–12 base multiplex identifier (MID) tag in the 5' end (at least four differences to each other). PCR was performed in four replicates for each primer pair using 25 cycles. The amplicons were checked for the presence of a product on 1% agarose gel. In case of no visible band or a strong band, we repeated the amplification program by adjusting the number of cycles between 25 and 35. The PCR products were purified using Exo-Sap enzymes (Sigma, St. Louis, MO, USA), and 20 µl of the purified PCR product was normalized using a Sequalprep™ Normalization Plate (96) Kit (Invitrogen Inc., Carlsbad, CA, USA) according to the manufacturer's instructions. The PCR products were pyrosequenced using the Roche GS FLX+ platform and Titanium chemistry in LGC Genomics (Berlin, Germany). Raw sequence data and associated metadata are available in UNITE repository.

Bioinformatics and phylogenetic analyses

Pyrosequencing reads (**IV**, **VI**, **VII**) were cleaned based on the quality information using Mothur 1.30.2 denoising algorithm (Schloss et al. 2009). Short sequences (<300 bp in length) and sequences possessing any mismatch to the primers were removed using the SEED 1.2.3 platform (Větrovský and Baldrian 2013). Sequences were demultiplexed based on the primer tags. Only reverse sequences from ITS4 were used for the subsequent data processing. Putative chimeras were identified and removed, and the remaining sequences were pooled and clustered into OTUs with USEARCH (Edgar et al. 2011) using 97% similarity level. We removed all global singletons, because nearly half of these are suggested to be artificial (Tedersoo et al. 2010). The remaining OTUs were taxonomically identified based on representative sequences using Biopython scripts for running BLASTn queries against the INSDc and UNITE. All sequences belonging to plants or other non-fungal groups were excluded from the dataset. We typically relied on 90, 85, 80, and 75% sequence identity as a criterion for assigning OTUs with names of a genus, family, order, or class, respectively. Representative sequencing of fungal OTUs (those with e-value $\geq e^{-50}$) were assigned to species hypothesis (SH) using UNITE (Kõljalg et al. 2013).

We assigned putative fungal ecology to obtained OTUs based on their taxonomic placement (**VI**, **VII**). The rough division of fungal OTUs into two ecological guilds, endophytic fungi (EndF) and putative ErMF was chosen, because the ability to form ericoid mycorrhizal symbiosis is not phylogenetically conserved among fungal species. In Helotiales, well known ErMF species are closely related to EcMF as well as non-mycorrhizal symbionts. On the contrary, many fungal taxa belonging to Helotiales, but distinct from the known ErMF species from the PEA, have been described as putative ericoid mycorrhizal symbionts (e.g. Grelet et al. 2009; Zhang et al. 2009). The ability to

form ericoid mycorrhizal symbiosis shows a similarly low phylogenetic signal in Sebacinales as well (Weiss et al. 2013). The third sufficiently confirmed group of ericoid mycorrhizal fungi belongs to Hymenochaetales (Kolařík and Vohník 2018). Therefore, fungal OTUs belonging to these three taxonomic groups were considered as putative ErMF.

Phylogenetic methods were used for more reliable identification of fungal isolates (**II**, **III**) or OTUs (**IV**, **V**, **VI**). Further sequences, derived preferentially from cultured isolates deposited in international culture collections, as well as suitable outgroup taxa were retrieved from INSDc to represent the genetic variability of the isolates or OTUs as comprehensively as possible. Sequences were aligned using the iterative refinement method of MAFFT (L-INS-i; http://mafft.cbrc.jp/alignment/server/). The alignment was checked and corrected manually using BioEdit V7.0.0 (Hall 1999). For phylogenetic analyses, maximum likelihood (ML) and Bayesian methods of inference were applied using MEGA 7 (Kumar et al. 2016) and MrBayes v3.2.6 (Ronquist and Huelsenbeck 2003). The ML analysis was done using GTR model with uniform rates among sites and NNI tree inference option. The Bayesian analysis was performed using the GTR substitution model with gamma distributed rate across the sites.

Statistical analyses

To test differences in colonization levels and root or shoot biomass production among experimental treatments (**II**, **III**, **IV**) we used the STATISTICA 12 software (StatSoft Inc., USA). Preferentially, we used parametric methods such as ANOVA. However, if the data did not meet the criteria of normal distribution and homogeneity of variances, the non-parametric Kruskal-Wallis test followed by a multiple-comparison z-value test were used.

To determine the drivers of fungal richness in Ericaceae-associated fungal communities (**IV**, **VI**, **VII**), we randomly subsampled the number of sequences per sample into the lowest number of sequences per sample, a procedure termed rarefaction. The general least squares (GLS) model was built to identify the main predictors of OTU richness, based on tested environmental variables using a routine implemented in the nlme package of R (Pinheiro et al., 2016). The best model was selected according to the corrected Akaike information criterion (AICc). Robustness of the best model was further evaluated by averaging models that fell into the 95% AICc confidence set.

Hellinger transformation was used to standardize fungal OTU abundance data across samples, whereas Bray-Curtis distance was used for computing dissimilarity matrices. The spatial distances between samples were included into subsequent analysis by reducing the Euclidean distance matrix into spatial Principal Coordinates of Neighbourhood Matrix (PCNM) vectors (Borcard and Legendre 2002). To address the relative importance of environmental factors and spatial distances between the samples on the fungal community structure,

we used PERMANOVA (**VI**, **VII, VIII)** as implemented in the adonis routine of the vegan package of R (Oksanen et al. 2012). Adonis tests the significance of discrete and continuous factors based on permutations. Adjusted R^2 was calculated based on the adonis results. Using the Bray-Curtis distance, we also constructed non-metric multidimensional scaling (NMDS) plots in the Ecodist package of R (Goslee and Urban 2007) for visualizing trends in fungal communities. Confidence ellipses for NMDS plots were calculated by the function ordiellipse in Vegan package. Indicator OTUs for different environments were determined using "indVal" function of the labdsv package of R (Roberts 2014), where the significance of indicator values is determined based on a permutation test. Only OTUs found in more than four samples were included in the analysis.

To assess network properties (**VIII**), we calculated nestedness and modularity metrics based on plant–fungi co-occurrence matrices. The modularity index of each dataset was calculated using a simulated annealing algorithm as implemented in NetCarto software (Guimerá & Amaral, 2005). We calculated the nestedness metric based on overlap and decreasing fill using the NODF function in the bipartite package of R. To test for differences among fungal guilds in host effect, nestedness and modularity, we applied a nonparametric multiple comparison procedure with an unbalanced one-way factorial design as implemented in the gao_cs function in the nparcomp package of R (Gao et al., 2008).

RESULTS AND DISCUSSION

Identification of ericoid mycorrhizal fungi

The study **I**, focused on occurrence of plant-fungal symbiotic life-styles among fungi, comprised 183,208 fungal ITS sequences. Of these, 28,791 (15.7%) sequences belonged to EcMF and 3,176 (1.7%) to AMF. In total, 1,457 (0.8%) and 2,267 (1.2%) sequences were recovered from roots of ErM plants and orchids, respectively. Metadata on interacting taxon were available for 6,272 (21.8%), 835 (26.3%), 1,093 (75.0%) and 1,608 (70.9%) entries of EcM, AM, ErM and OrM fungi, respectively. In AMF, plant roots, spores and soil contributed 41.2%, 33.9% and 19.0% to the source of isolation, respectively. In EcMF, fruit bodies, ectomycorrhizas and soil DNA accounted for 43.3%, 32.4% and 14.6% of the identification sources, respectively. In contrast to EcM and AM mycobionts, the fungi inhabiting roots of ericoid plants were identified directly from roots with or without a culturing step. In putatively ErMF, 690 (47.4%) sequences were obtained directly from ErM roots and 767 (52.6%) sequences were obtained from living cultures. In the cultured isolates, we could trace the symbiotic performance of 226 isolates in various experiments. Taken together, 60.2% of the isolates were capable of forming coils and/or stimulating growth of ericoid plants in vitro. More than 95% of the functional ErM mycobionts belonged to the Helotiales. Cultures identified as Hypocreales and Coniochaetales probably represent fast-growing contaminants, because these taxa have never been suggested as functional partners in ErM. While taxa from all fungal phyla have been identified from roots of ericoid plants, experimental evidence for functional association covers only a few, albeit large, groups of fungi. The remaining DNA-based identified taxa may belong either to un-culturable mycorrhizal fungi or to non-mycorrhizal guilds of opportunistic pathogens, endophytes or saprobes (Allen et al. 2003; Walker et al. 2011). As an alternative to direct synthesis experiments, electron microscopy may provide in situ evidence for functional associations between plants and fungi at higher taxonomic levels (Moore et al. 1978).

A yet undescribed type of ericoid mycorrhizal association in *Vaccinium* spp. was observed in field-collected roots from semi-natural blueberry plantation in Norway (**II**). Its most prominent characteristic is a dense layer of clamp-bearing hyphae over the surface of terminal parts of young hair roots. The hyphae comprising the sheath were of variable diameter and penetrated epidermal cells, forming dense hyphal coils typical for ericoid mycorrhizae. Three isolates with distinct morphology and/or growth rate were obtained from 30 sheathed ErM roots. Both clamped basidiomycetes JPK 87 and JPK 90 grew well on MMN producing dense whitish colonies. The basidiomycete JPK 90 formed a long branch residing as sister to Trechisporales (PP = 0.98) in MB analyses, but being inconsistently clustered with Trechisporales, Hymenochaetales or Russulales in ML trees. Recent study, based on protein coding sequences and

morphology, placed the isolates within the Hymenochaetales order (Kolařík and Vohník 2018). On soil agar, sheathed ErM formed by the basidiomycetes JPK 87 and JPK 90 occurred in, but were not limited to, root apices and did not appear to follow a predictable pattern among root orders. The extent of intracellular colonization among inoculated plants was highly variable (coefficient of variation = 1.7). Significant correlations between ErM intracellular colonization and shoot length ($r = 0.74$, $p = 0.002$) and shoot weight ($r = 0.54$, $p = 0.04$), along with negligible shoot growth of non-(ErM)-colonized and non-inoculated control plants, indicate that colonization by the basidiomycetes JPK 87 and JPK 90 positively contributed to shoot growth. It is generally observed that ascomycetous ErM fungi do not produce developed extraradical hyphal mantles around colonized roots; so far the only described symbiosis of Ericaceae characteristically possessing hyphal mantles is cavendishioid ectendomycorrhiza. However, this symbiosis is formed by nonclamped hyphae of Sebacinales and its mantles are accompanied by intercellular fungal tissue resembling a Hartig net (Binder et al. 2005).

To determine the ecological interactions of ErMF (**III**), we focused on ascomycetes associating with basidiomycetous ectomycorrhizas of *Picea abies* in a temperate montane forest in central Europe, where ericoid shrubs dominate in forest understory. The 360 surface-sterilized basidiomycetous ectomycorrhizas yielded 128 relatively slow-growing non-sporulating isolates. Most of the isolates belonged to the PEA encompassing *Cadophora finlandica*, *Meliniomyces bicolor*, *M. variabilis* and two unidentified ascomycetous isolates. In the resynthesis experiments, none of the *M. bicolor* nor *M. variabilis* isolates formed ectomycorrhiza or ectendomycorrhiza with spruce seedlings, but rather produced intracellular colonization in the root cortex cells which was usually accompanied with apparent darkening and thickening of their cell walls. In the same sampling sites, *M. variabilis* did not belong among the major soil fungal OTUs (Baldrian et al. 2012). These observations suggest that *M. variabilis* is an obligate biotroph rather than a free-living soil dweller. Additionally, *M. variabilis* seems to have the broadest ecological niche among the PEA members – it has been detected as an endophyte in the roots of a taxonomically diverse spectrum of plants including Fagaceae, Orchidaceae and Salicaceae (Hambleton and Sigler 2005), Betulaceae and Pinaceae (Kernaghan and Patriquin, 2011) and Poaceae and Primulaceae (Tejesvi et al. 2013), but seems to prefer Ericaceae, the only group which forms true mycorrhizas with *M. variabilis*. Except for one *M. variabilis* isolate, all the remaining PEA isolates colonized roots of *V. myrtillus* intracellularly. Most of the PEA isolates formed dense intracellular hyphal coils resembling ericoid mycorrhiza, including *C. finlandica* and *M. bicolor*. *C. finlandica* and *M. bicolor* have been previously detected as EcM co-associated fungi but they also form characteristic ecto- and ectendomycorrhizas (Wang &Wilcox 1985; Vralstad et al. 2000, 2002; Villarreal-Ruiz et al. 2004). Additionally, both species have been shown to form structures resembling ericoid mycorrhizas in vitro (Vralstad et al. 2002; Villarreal-Ruiz et al. 2004), but they are only rarely detected in

Ericaceae roots under natural conditions. Therefore, the potential of PEA fungi to potentially form common mycorrhizal mycelial network between ErM and EcM plants, seems to be rather ecologically insignificant.

The dual mycorrhizal ability of other Helotiales species (with affinity to *Phialocephala fortinii* s. l.—*Acephala applanata* species complex, PAC), that may form mycorrhizal links between Ericaceae and Pinaceae, was tested in resyntheses experiments in the subsequent study (**IV**). Roots of all inoculated plants (*P. abies* and *V. myrtillus*) possessed intraradical fungal colonization. All species belonging to PAC formed intracellular microsclerotia consisting of melanised or hyaline hyphae in both *P. abies* and *V. myrtillus*. In *P. abies*, microsclerotia were often found within the central stele. *Acephala macrosclerotiorum* colonized spruce intercellulary and formed a Hartig net and a parenchymatous hyphal net on the root surface resembling a loose hyphal mantle. This species formed darkly pigmented sclerotia on the surface of some roots, as previously showed by Münzenberger et al. (2009). Intracellular hyphal coils resembling ErM together with intracellular microsclerotia typical for endophytic colonization were observed in blueberry roots colonized by *A. macrosclerotiorum*. Therefore, *A. macrosclerotiorum* may potentially form a mycorrhizal link between *P. abies* and *V. myrtillus*. To test the occurrence of *A. macrosclerotiorum* in Ericaceae plants in situ, we chose a forest ecosystem where *A. macrosclerotiorum* dominates on *Pinus sylvestris* roots. Using direct isolation of DNA from Ericaceae roots with subsequent 454-sequencing of fungal ITS rDNA region, we did not obtain any sequences similar to *A. macrosclerotiorum*. It remains questionable, if mycorrhizal links between Ericaceae and Pinaceae occur in temperate or boreal forests.

Community composition of ericoid mycorrhizal fungi

The communities of Ericaceae root-associated fungi were significantly affected by environmental factors such as elevation gradient (**VI**, **VII**), host plant species (**VII**, **VIII**) as well as soil moisture content (**VI**). On the larger spatial scales, ericoid mycorrhizal fungi showed biogeographical patterns (**V**).

Although the ericoid mycorrhiza represents ecologically important symbiotic partnership, its global distribution has never been assessed previously (**IV**). In spite of the very broad distribution of the ErM plants (all continents except Antarctica), there are also many areas where ErM plants are missing, such as large parts of South America, SW Asia, and much of Africa and Australia. Compared to ErM host plants, much less is known about the distribution and global biogeography of their root-associated mycorrhizal symbionts. Traditionally, most of the studies focused on the diversity and community ecology of ErMF were performed on the Northern Hemisphere, particularly in Europe and North America. Preliminary insights indicate that some ErMF species (*Pezoloma ericae*) have a very broad distribution range. On the contrary, some

species have much narrower distribution range restricted to a single hemisphere (*Meliniomyces variabilis*) or continent (*Cairneyella variabilis*).

In the study **VII**, which focused on community ecology of Ericaceae roots associated fungi in Papua New Guinea, 670 OTUs were recovered from 24,008 sequences that passed through the denoising steps and removal of singletons and non-fungal sequences. The PERMANOVA test revealed significant effects of elevation and spatial vectors on putative ErMF and EndF community composition. Both variables (elevation and space) explained more variation in putative ErMF than EndF communities. The observed pattern in our study was mostly caused by the highest elevation site, which showed the greatest relative abundance of Helotiales. Broad ecological niche of the Helotiales species is well documented by numerous studies, describing them as abundant members of fungal communities from many different environments such as neotropical forests (Haug et al., 2004), glacier forefronts (Brown and Jumpponen, 2014), sub-Antarctic islands (Upson et al., 2007), or roots of submerged aquatic plants (Kohout et al., 2012). On the other hand, the second most widespread and well known ErMF order, Sebacinales (Weiss et al., 2004), showed higher occurrence in the lowest-elevation sites. High relative abundance of Sebacinales associated with Ericaceae roots was also found in other tropical mountain regions (Setaro and Kron, 2011), although our study is the first one focusing on sites above 2500 m.a.s.l. These findings support the ubiquity of Sebacinales and their worldwide distribution (Oberwinkler et al., 2013; Tedersoo et al., 2014b). On the main study site, which was used to study host plant effect on Ericaceae associated fungal communities in Papua New Guinea, PERMANOVA analysis revealed a substantially different effect of Ericaceae host plant taxonomy on EndF and putative ErMF communities. While putative ErMF communities were significantly affected by host plant genus, EndF communities differed between host plant subfamilies. These results show that host plant taxonomic levels above the species level (Kjøller et al., 2010; Walker et al., 2011) play an important role in structuring EndF communities rather than putative ErMF communities. Differentiation of ErMF communities at lower taxonomic levels may promote coexistence of Ericaceae genera, if ErMF for example differ in exploitation of different nutrient sources (Cairney et al., 2000).

In study **VI**, which focused on community ecology of root-associated fungi of *Erica dominans* in Drakensberg Mountains in South Africa, 353 OTUs were recovered from 11,813 sequences which passed through the denoising steps, and removal of singletons and non-fungal sequences. Ascomycota dominated in the roots of *E. dominans* in most of the samples. We identified two OTUs corresponding to PEA, which represented approx. 2% of sequences in the whole dataset and occurred in 10 out of 15 samples. The rest of OTUs with high similarity to PEA clustered with *Meliniomyces* sp. 2, which belongs to the Clade 4 of PEA according to Hambleton and Sigler (2005). For the first time, we demonstrated the well-known ErMF *P. ericae* in Ericaceae roots in Africa. Although *P. ericae* has been frequently documented in Ericaceae roots from the Northern Hemisphere (e.g., Bougoure et al. 2007; Kjøller et al. 2010; Gorzelak

et al. 2012), it was so far mostly detected in non-Ericaceae plants and rhizoids of leafy liverworts in Antarctica or Chile (Chambers et al. 1999; Upson et al. 2007; Upson et al. 2009). The only record of *P. ericae* in Ericaceae roots from the Southern Hemisphere comes from a recent study in Patagonia (Bruzone et al. 2016). Taken together, *P. ericae* represents the most widespread fungal species (so far not detected only in Australia) with ericoid mycorrhizal lifestyle. *Erica dominans* root fungal communities were structured by geographical distance, altitude as well as microhabitat (dry vs. wet sites). We detected several fungal taxa which distribution was significantly affected by microhabitat type. Only the OTU0005, matching with *Meliniomyces* sp. 2 from *P. ericae* aggregate, was significantly more common in dry sites.

Based on synthesis on 111 independent sampling units from 44 published studies and five unpublished datasets, we did not find any significant difference in response between ErMF and other fungal guilds to host plant identity (**VIII**). The only exception was represented by OrM fungal communities, which responded most strongly to the identity of their host plants. Orchid and ericoid mycorrhizal fungal communities were also more modular than EcMF and EndF communities, with AMF in an intermediate position. Compared to EcMF symbionts with multiple examples of high unilateral or reciprocal specialization in EcM symbiosis, such as *Alnus* and *Alnus* associated fungi or *Pinus* and Suillaceae, (Bruns et al., 2002; Kennedy et al., 2015), the average host effect on ErMF community composition was comparable, although such examples of specificity are not known for ErMF symbiosis. Interestingly, the relatively low level of host effect in ErM associations contrasts with the high modularity among this group. Such contrasts between modularity and host effect have been reported previously, possibly deriving from the sensitivity of the modularity measure to the total links in the dataset (Bahram et al., 2014).

CONCLUSIONS

The following main conclusions can be inferred from my thesis:

- In the cultured isolates, more than 95% of the functional ErM mycobionts belonged to the Helotiales.
- Novel lineage of basidiomycete formed characteristic sheathed ErM symbiosis with mantle resembling a Hartig net and enhanced growth of *Vaccinium* spp. in vitro, and showed ability to degrade a recalcitrant aromatic substrate.
- Fungi belonging to the *Pezoloma ericae* aggregate co-associate as endophytes with ectomycorrhizas of *Picea abies* in a temperate montane forest in central Europe, where ericoid shrubs dominate in forest understory. Most of the PEA isolates formed dense intracellular hyphal coils resembling ericoid mycorrhiza in roots of *V. myrtillus*. Therefore EcM roots may represent an important refuge for ErMF.
- We found the ability of *Acephala macrosclerotiorum* to form EcM symbiosis with *P. abies* as well as ErM symbiosis with *V. myrtillus* based on resynthesis experiments in laboratory conditions. However, we did not detect any sequences similar to *A. macrosclerotiorum* in Ericaceae roots, although *Acephala macrosclerotiorum* dominated on surrounding EcM roots in natural forests. It remains questionable, if *Acephala macrosclerotiorum* may serve as a common mycorrhizal network between Ericaceae and Pinaceae in temperate or boreal forests.
- The communities of Ericaceae root-associated fungi were affected by environmental factors such as elevation, host plant species as well as soil moisture-related microhabitat, indicating the presence of multi-scale environmental filtering. On the global scale, ericoid mycorrhizal fungi showed strong biogeographical patterns. While some ErM fungal species (*Pezoloma ericae*) have a very broad distribution range, other species have much narrower distribution range restricted to a single hemisphere (*Meliniomyces variabilis*) or continent (*Cairneyella variabilis*). This suggests that also conidial microfungi can be limited by long-distance dispersal capacity and sometimes more than the host plants.

SUMMARY

Mycorrhizal symbiosis is a mutualistic partnership between plants and fungi that represents one of the oldest and the most widespread symbioses on the Earth. One of the youngest mycorrhizal type is ericoid mycorrhizal (ErM) symbiosis, a mutualistic relationship formed between species belonging to several lineages of the Ericaceae family and diverse group of soil fungi. Ericoid mycorrhiza is characterized by the intensive fungal colonization of the outermost root cell layer. Mycorrhizal fungi form a coiled intracellular hyphal complex. Ericoid mycorrhizal plants often occur on extremely poor soils, where most of the nutrients are locked up in complex forms of soil organic matter, with restricted biological availability. The ErM symbiosis represents a key evolutionary adaptation of ErM plants to mobilize the nutrients from such recalcitrant substrates. However, ErM remains largely overlooked compared to the more common mycorrhizal types, such as arbuscular mycorrhiza and ectomycorrhiza, and a broader general understanding of the ErM symbiosis is lacking. While arbuscular mycorrhizal fungi have a monophyletic origin, the ability to form ErM as well as ectomycorrhiza evolved independently multiple times in several fungal lineages. The ERM fungi belong to several fungal lineages of Ascomycota as well as Basidiomycota. Nowadays, there are few sufficiently proven ErM fungi, which belong to four taxonomic groups, Helotiales, Chaetothyriales (Ascomycota) and Sebacinales and Hymenochaetales (Basidiomycota). In this thesis, I focus on Ericaceae associated fungi from various aspects of the partnership, because the ericoid mycorrhizal symbiosis is probably the most overlooked mycorrhizal symbiotic type. Firstly, this thesis aims to determine the occurrence of ericoid mycorrhizal life-style among fungi. Furthermore, I also focused on determination of environmental factors which significantly affect composition of fungal communities associated with roots of ericoid mycorrhizal plants. To determine the occurrence of ericoid mycorrhizal life-style among fungi, we isolated root associated fungi from sampled Ericaceae plants or seedlings of *Picea abies* from sampling sites in Norway or Czechia. Ecological lifestyle of isolated fungi was assessed in number of resynthesize experiments. To determine the environmental factors, which affect composition of fungal communities associated with roots of ericoid mycorrhizal plants, we sampled roots of Ericaceae plants on Mount Wilhelm in Papua New Guinea and in Drakensberg mountain range in the Republic of South Africa. I used the 454 pyrosequencing method to determine fungal communities associated with the Ericaceae roots.

The main results and conclusions are the following: 1) Novel lineage of Basidiomycota formed characteristic sheathed ErM symbiosis with mantle resembling a Hartig net and enhanced growth of *Vaccinium* spp. in vitro, and showed ability to degrade a recalcitrant aromatic substrate. 2) Most of the *Pezoloma ericae* aggregate isolates associated with *Picea abies* formed dense

intracellular hyphal coils resembling ericoid mycorrhiza in roots of *V. myrtillus*. 3) We found the ability of *Acephala macrosclerotiorum* to form EcM symbiosis with *P. abies* as well as ErM symbiosis with *V. myrtillus* based on resynthesis experiments in laboratory conditions. 4) The communities of Ericaceae root-associated fungi were affected by environmental factors such as elevation, host plant species as well as soil moisture-related microhabitat, indicating the presence of multi-scale environmental filtering. 5) On the global scale, ericoid mycorrhizal fungi showed strong biogeographical patterns. While some ErM fungal species (*Pezoloma ericae*) have a very broad distribution range, other species have much narrower distribution range restricted to a single hemisphere (*Meliniomyces variabilis*) or continent (*Cairneyella variabilis*).

SUMMARY IN ESTONIAN

Erikoidse mükoriisa ökoloogia

Sümbioos mükoriisa ehk seenjuure vahendusel on üks vanimaid ja enim levinud mutualismivorme maailmas. Mükoriissetes suhetes seenpartner varustab taime vees lahustunud mineraalainetega ning saab taimelt vastu suhkruid. Erikoidne mükoriisa (ErM) on arbuskulaarse mükoriisa ja ektomükoriisa kõrval evolutsiooniliselt noorim mükoriisatüüp. Taimed sugukonnast kanarbikulised (Ericaceae), kuhu kuuluvad ka mustikas, pohl ja kanarbik, moodustavad ErM sümbioosi mitmete rühmade mullas ja juurtes elavate endofüütsete seentega. Seenehüüfid kasvavad taime juurerakkudesse sisse ja moodustavad paunakesi – ajukujulisi struktuure, kus taime rakumembraani ja seeneraku piirpind on oluliselt suurenenud toitaainete vahetuse soodustamiseks. Kanarbikulised esinevad sageli vaestel happelistel muldadel, kus toitained on peamiselt orgaanilisel kujul ja raskesti taimedele omastatavad. Kanarbikuliste peamine ökoloogiline kohastumus ongi mükoriisaseente abil makro- ja mikroelementide kättesaamine. Kanarbikulised on metsanduse ja põllumajanduse aspektist väheolulised, mistõttu ErM ökofüsioloogia ja sellega seotud seente elurikkust on vähe uuritud võrreldes teiste mükoriisatüüpidega. Senised elurikkuse uuringud ja mükoriisa sünteesi katse näitavad, et ErM moodustavad seened kuuluvad mitmesse kottseente (*Helotiales, Chaetothyriales*) ja kandseente (*Sebacinales, Hymenochaetales*) seltsidesse. Oma väitekirjas keskendun erinevatele aspektidele ErM seente elurikkuses ja ökoloogias, eelkõige keskkonnaparameetritele, mis mõjutavad seenekooslusi. ErM seente tuvastamiseks isoleerisin kanarbikuliste ja hariliku kuuse juurtes kasvavad seened puhaskultuuri Tsehhimaa ja Norra metsadest ning viisin läbi mükoriisa sünteesi katsed laboris. ErM seente kooslusi mõjutavate keskkonnaparameetrite tuvastamiseks kogusime kanarbikuliste juuri Mount Wilhelmi mäelt Paapua Uus-Guineas ja Drakensbergi mägedest Lõuna-Aafrika Vabariigis. Kasutasin Roche 454 pürosekveneerimise tehnoloogiat sealt kogutud juurtelt seente määramiseks.

Minu väitekirja peamised tulemused ja järeldused on järgmised: 1) senimääramata kandseente haru moodustab erikoidset mükoriisat, kus taimerakkude pinnal areneb õhuke seeneniidistiku kiht ja seen soodustab mustika kasvu ning lagundab aromaatseid polümeere; 2) kuusejuurtelt isoleeritud seened *Pezoloma ericae* liigikompleksist on võimelised moodustama erikoidsele mükoriisale iseloomulikke struktuure mustika juurerakkudes; 3) seeneliik *Acephala macrosclerotiorum* moodustab ektomükoriisat hariliku kuusega ja erikoidset mükoriisat mustikaga laboritingimustes; 4) kanarbikuliste seenekooslusi mõjutavad paljud keskkonnaparameetrid, eelkõige kõrgus üle merepinna, peremeestaime liik ning mikroelupaik niiskuse gradiendil; 5) geograafiline kaugus globaalsel skaalal: mõnel seenerühmal on väga lai levik (*Pezoloma ericae*), ent teised on piiratuma levilaga (*Meliniomyces variabilis* ja *Cairneyella variabilis*).

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PUBLICATIONS

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